The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Tremataspididae)

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Synopsis

Various aspects of the morphology of the osteostracan *Sclerodus* Agassiz are described and discussed in the light of new specimens in an attempt to reconcile four different morphological interpretations. It is concluded that *Sclerodus* has normal osteostracan sensory fields, that the lateral line system may be represented as a series of pits, and that the margin of the cephalothoracic shield is penetrated by four fenestrae which may possibly have served a stabilizing hydrodynamic function. Relationships of *Sclerodus* are discussed with a review of osteostracan classification leading to discussion of computer-generated trees. A phylogeny is favoured which treats ateleaspids as a paraphyletic group and tremataspids as a monophyletic derived group.

Introduction

Sclerodus pustuliferus Agassiz is a small and rather unusual osteostracan restricted to the Downtonian of the Anglo-Welsh basin. Remains of *Sclerodus* are very common in the Ludlow Bone Bed and immediately overlying rocks, where it is easily recognized by its distinctive ornament of small, closely-packed hemispherical tubercles. However, the abundance of its remains is matched by our ignorance of its morphology. Only the dorsal half of the cephalic armour is known, and even here knowledge is incomplete. There are very few reasonably intact specimens and regrettably one of the best (Stensiö 1932: pl. 52, fig. 2) has now been lost. The fragments most commonly found are pieces of the main part of the shield and portions of the so-called 'cornua'. Each 'cornu' bears a marginal row of elongate tubercles, so that fragments of them were initially confused with jaws and teeth. More complete material enabled Lankester (1870) to confirm a suggestion made by Harley (*in* Murchison 1867) that *Sclerodus pustuliferus* is, in fact, an osteostracan and to provide the first restoration (Lankester 1870: fig. 31). Since that time three further restorations have been attempted (Stensiö 1932, Denison 1951*a*, Janvier 1975). No two of these agree on interpretation of structures which are obvious in other osteostracans, such as the presence or absence of cornua, pectoral sinuses or one or more lateral sensory fields.

These discrepancies, combined with the fact that *Sclerodus* shows some interesting special-izations along the rim of the cephalothoracic shield, make this monotypic genus an interesting subject for study. The main motivation derives from sporadic collecting in the Ludlow Bone Bed at Forge Bridge, Downton Castle estate, Shropshire by Dr W. Graham-Smith of Boars Hill, Oxfordshire. Dr Graham-Smith has collected many fragments of *Sclerodus*, some of which show unusual and previously undescribed pits surrounding the orbits. One specimen, BMNH P.58694, described and illustrated here (Fig. 5, p. 11), was particularly helpful in the reinterpre-tation of existing material. I am grateful to Dr Graham-Smith for the donation of several specimens. It has allowed me to redescribe and update our knowledge of *Sclerodus* and to offer comments on some of the more unusual aspects of this genus.

Historical review

Sclerodus pustuliferus was first described by Agassiz (*in* Murchison 1839: 606; pl. 4) from figures, sent to him by Murchison, of four fragmentary specimens. On the basis of these figures Agassiz likened the fragments to the grinding teeth of the 'bradyodont' *Psammodus*, and because of the rough pustulated surface he coined the name *Sclerodus* (rough-tooth) *pustu-liferus*. On the same occasion Agassiz described seven further specimens as jaws and teeth under the names *Plectrodus mirabilis* and *Plectrodus pleiopristis*.

M'Coy (1853) reinterpreted nearly all the specimens figured by Murchison (1839: pl. 4), including those referred to species of the genera *Sclerodus* and *Plectrodus*, as being the remains of the crustacean *Pterygotus*. Additionally, he could see no reason to recognize separate species and united them all under the name *Pterygotus pustuliferus* (= *Plectrodus mirabilis* + *P. pleiopristis* + *Sclerodus pustuliferus*). It should be noted that M'Coy (1853: 13) apparently did not see the original material referred to those species because it had by then been 'lost' (see below).

Murchison (1853) replied testily, saying that he, and Messrs Salter and J. Sowerby, who had prepared the drawings sent to Agassiz, disagreed with the crustacean interpretation and main-tained the identity of these remains as fish jaws and teeth. Egerton (1857) followed by describ-ing more material from Ludlow as jaws of *Plectrodus mirabilis*. Thus, while authors disagreed over whether there were one or more species, almost all agreed that they were fishes and not crustaceans. This was confirmed by Harley (1861: 544, footnote) who had sectioned specimens and found them to be made of bone and dentine. Harley further suggested that they were the posterior spines (cornua) of cephalaspid fishes rather than fish jaws and teeth. Murchison, while acknowledging Harley's opinions (1867: pl. 35, legend), remained convinced that they were jaws and ankylosed teeth (1867: 241).

Lankester (1870: 58) supported Harley's view by describing tolerably complete head shields based on new material collected by Dr Grindrod and Mr Lightbody from the Downton Castle Sandstone of Ludford Lane, Ludlow. Lankester regarded *Plectrodus mirabilis* and *P. pleiopristis* as junior synonyms of *S. pustuliferus* and considered *Sclerodus* as a subgenus of *Auchenaspis* Egerton. He named this subgenus *Eukeraspis*, but he gave no reason why he dropped the name *Sclerodus*. *Eukeraspis* was associated with *Thyestes* (*Auchenaspis*) because Lankester believed that in both the shield was composed of a semicircular cephalic porton and an abdominal portion formed by separate paired plates. The abdominal portion was unknown for *Eukeraspis*, but Lankester predicted its presence, adding (1870: 59) '. . . this is a question which inquiry with the hammer may soon decide . . .'. Such inquiry has failed to find the abdominal division, but from Lankester's time *Sclerodus* has been closely associated with *Auchenaspis* (*Thyestes*). Nevertheless, Lankester (1870: fig. 31) did provide the first restoration of the cephalic shield.

Woodward (1891) agreed with Lankester over the restoration, association with *Thyestes*, and renaming *Eukeraspis*. But Woodward considered *Eukeraspis* to form a distinct genus (syn. *Sclerodus*, *Plectrodus*).

Thus, to this point in the confused history of *Sclerodus* there had been debate about whether the Ludlow Bone Bed material represented one, two or three species; whether it belonged to fishes or to crustaceans; whether it represented jaws and teeth or part of the cephalic shield;

and finally, whether the generic name should be changed to *Eukeraspis*. By the turn of the century the consensus seemed to be that there was one species, that it was a cephalaspid fish closely related to *Thyestes* and that the original material described by Agassiz represented the denticulated cornua and should go under the name of *Eukeraspis*.

Woodward (1917) considerably clarified the situation by following through his earlier suspicion (1891: 195) and a suggestion by Priem (1910: 5) that *Plectrodus mirabilis* and *P. pleiopristis* represented the dentigerous jaws of ischnacanthid acanthodians. This is the current status of *Plectrodus* (Denison 1979: 41). Thus, *Sclerodus pustuliferus* remains the only cephalaspid material described by Agassiz in Murchison's *The Silurian System*. The change of generic name to *Eukeraspis* is unnecessary (see also Stensiö 1932: 175, footnote).

Subsequent work on *Sclerodus* is chiefly that of Stensiö (1932), who has provided the most complete description, Denison (1951*a, b*) and Janvier (1975). These authors differ in their interpretations of the 'cornua' and sensory fields and their ideas are discussed in the relevant descriptive sections below. A summary of the differing ideas of the morphology is provided in Fig. 1.
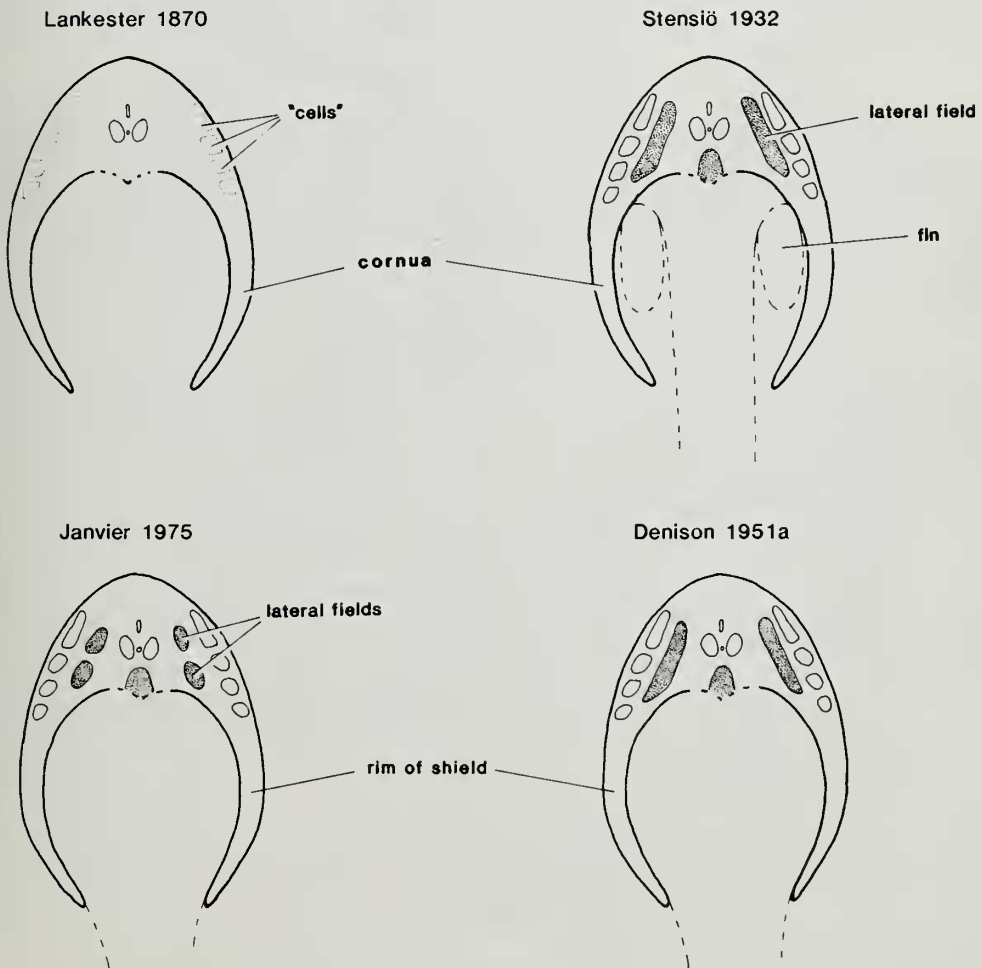

Fig. 1 *Sclerodus pustuliferus* Agassiz. Four morphological interpretations.

As described above, the early history of the study of *Sclerodus* was somewhat tangled. Unfortunately, the history of the original material is equally problematical. When Agassiz described *Sclerodus* and *Plectrodus* he did so from drawings. Murchison (1853), in his reply to M'Coy (see above), records that he had given the specimens, collected and mounted on cards by Rev. R. W. Evans, to the Geological Society of London. But he also records that the specimens could no longer be found (see also Murchison 1867: 133, footnote). So, sometime between 1839 and 1853 some of the specimens illustrated in plate 4 of *The Silurian System* had gone astray. It appears (Jeannet 1928) that some of the material was incorporated in the Musée d'Histoire Naturelle de Neuchâtel and later into the Institut de Géologie de l'Université de Neuchâtel where Agassiz taught, 1832–1846. It is possible that Agassiz, who visited England in 1840, or Joseph Dinkel, Agassiz' artist based at the Geological Society for several years, took some specimens to Neuchâtel with the intention of describing them more fully. But by then Agassiz was preoccupied with his glacial studies; in any event the descriptions were not forthcoming.

Woodward (1917: 74) found three of the original specimens in Neuchâtel in 1898 while Jeannet (1928: 106) records five of the original 11 specimens referred to *Sclerodus* and *Plectrodus*. There is only one of the four original specimens of *Sclerodus pustuliferus* and this is listed as number 3 and represents that illustrated in Murchison's *The Silurian System* (1839: pl. 4, figs 60–62). This was quite correctly chosen as the lectotype by Stensiö (1932).

Material and methods

The material studied belongs to the British Museum (Natural History) (BMNH); the British Geological Survey, Keyworth (BGS); and the Department of Geology, University of Birmingham (BU). The specimens are referred to by register number prefixed by their respective institutional abbreviations. Most of the material is from the Ludlow Bone Bed and was studied directly. Rubber latex casts were helpful in the study of the material from the Downton Castle Sandstone. Histological sections were made from isolated fragments found in the Ludlow Bone Bed.

Abbreviations used in figures

a.p	grooves housing anterior and posterior semicircular canals	o.a	foramen for occipital artery
a.pit	anterior pit	oes	groove for oesophagus
c.f	circumnasal fossa	orn	ornament
d	canal leading to dorsal sensory field	o.r	olfactory recess
d.a	groove for dorsal aorta	p.d	pineal duct
d.s.f	dorsal sensory field	p.f	prebranchial fossa
h.v	groove for lateral head vein (jugular vein)	p.o	pineal opening
		p.pit	posterior pit
i.c.a	foramen for internal carotid artery	prof	foramen for profundus nerve
l.s.f	lateral sensory field	v.c	vestibular chamber
m.f	marginal fenestra	v.s	superficial vein issuing from head vein
m.pit	middle pit	IV, V_2, VII, IX	cranial nerves
n.c	foramina for nerves		
n.d	nasohypophysial duct	1–4 s.e.l.	canals leading to lateral sensory fields (see p. 12)
n.o	nasohypophysial opening		
o	orbit		

Systematic description

Family **TREMATASPIDIDAE** Woodward, 1891

Genus *SCLERODUS* Agassiz, 1839

1839   *Sclerodus* Agassiz (in Murchison): 606.
1870   *Auchenaspis* Egerton (in part); Lankester: 58 (subgenus *Eukeraspis*).
1887   *Eukeraspis* Lankester; Zittel: 150.
1891   *Eukeraspis* Lankester (in part); Woodward: 193 (not *Plectrodus*).

DIAGNOSIS (emended). Tremataspids in which the circumnasal fossa is deep and elliptical, with a smooth floor: cephalothoracic shield perforated along lateral margin by four fenestrations, the largest lying anteriorly; thereafter each decreasing in size posteriorly: sensory lines absent, but perhaps represented by three pairs of pits lying close to the orbit and circumnasal fossa: abdominal region of the shield ossified along lateral margin only, leaving central part naked or perhaps covered with scales: ornament developed as regular hemispherical tubercles which are particularly large over the swellings immediately in front of and behind the pineal recess: margin of shield bearing a regular row of enlarged tubercles: histology of exoskeleton very simple, represented only by basal layer and overlying spongy bone with no circumareal canals.

TYPE AND ONLY SPECIES. *Sclerodus pustuliferus* Agassiz.

Sclerodus pustuliferus Agassiz

1839   *Sclerodus pustuliferus* Agassiz (in Murchison): 606; pl. 4, figs 27–32, 60–62.
1854   *Sclerodus pustuliferus* Agassiz; Murchison: pl. 35, figs 9–12.
1870   *Auchenaspis (Eukeraspis) pustulifera* (Agassiz); Lankester: 58, figs 31, 32; pl. 31, figs 9–14.
1932   *Sclerodus pustuliferus* Agassiz; Stensiö: 177, fig. 62; pl. 52, figs 1, 2; pl. 53, figs 1–5; pl. 56, fig. 1.
1951a   *Sclerodus pustuliferus* Agassiz; Denison: 185.
1975   *Sclerodus pustuliferus* Agassiz; Janvier: figs 2B, 5.

DIAGNOSIS. As for genus; the only species.

LECTOTYPE. Fragment of cornu: Institut de Géologie, l'Université de Neuchâtel number 3. Ludlow Bone Bed, Downtonian; Ludlow, Shropshire. Selected Stensiö (1932: 177).

MATERIAL. Fifty-five specimens were examined in this study, as detailed in Appendix, p. 27. The material comes from the Ludlow Bone Bed, Downton Castle Sandstone and Temeside Shales/Lower Red Downton Sandstone of Shropshire, Herefordshire and Staffordshire.

DESCRIPTION. The general shape of the shield is seen in BMNH P.9756, on which the restoration in Fig. 2 is based. The cephalic portion is strongly vaulted at the level of the orbits but the rim of the shield and so-called cornua are shallow.

There are few specimens which show the cephalic portion attached to the so-called cornua; more usually broken cephalic shields and isolated 'cornua' are found. One complete specimen (BMNH P.9756, Fig. 2) shows a total length of 45·5 mm, of which the cephalic portion is 21 mm long. Using the proportion of cephalic to 'cornu' length of this specimen one can estimate that the largest specimen (BGS GSM 5150) must have been about 85 mm in total length (snout to posterior level of 'cornua'). The greatest width occurs two-thirds of the way back and the outline of the head plus 'cornua' resembles that of *Dartmuthia* or *Tremataspis*.

The orbits are placed close together and this means that the pineal area is confined to a narrow longitudinal strip. No dermal pineal plate has been found and the extreme narrowness of the space left between the orbits may imply its absence. The pineal opening lies slightly below the surface where it opens at the end of a short duct within the skeleton (Figs 3, 5B, C). The duct is slightly asymmetrical which no doubt reflects the asymmetry of the underlying habenular recess as described by Janvier (1977) for *Belonaspis puella* (Wängsjö).

The anterior and posterior borders of the orbital area are raised into prominent ridges which bear ornament tubercles larger than those covering most of the shield. The anterior ridge runs into a crest surrounding the nasohypophysial opening, while the posterior ridge is continuous with a shallow ridge defining the dorsal sensory field (Fig. 3). The nasohypophysial opening is contained within the floor of a deep, well-defined depression—the circumnasal fossa (Stensiö 1932: fossa circumnasalis, Stensiö 1927; antorbital fossa, Lankester 1870). The nasohypophysial opening is slit-like and immediately surrounded by a narrow ridge of bone. The form of the circumnasal fossa is very similar to that seen in thyestidians (*sensu* Janvier 1981b) and especially to *Tremataspis* (Janvier 1985b: fig. 34A).

The nasohypophysial opening is an elongate slit similar to that seen in thyestidians. But it should be noted that a similarly-shaped opening is also seen in more plesiomorphic kiaeraspidians (Janvier 1981b). Such a shape implies that the hypophysial and nasal divisions are of
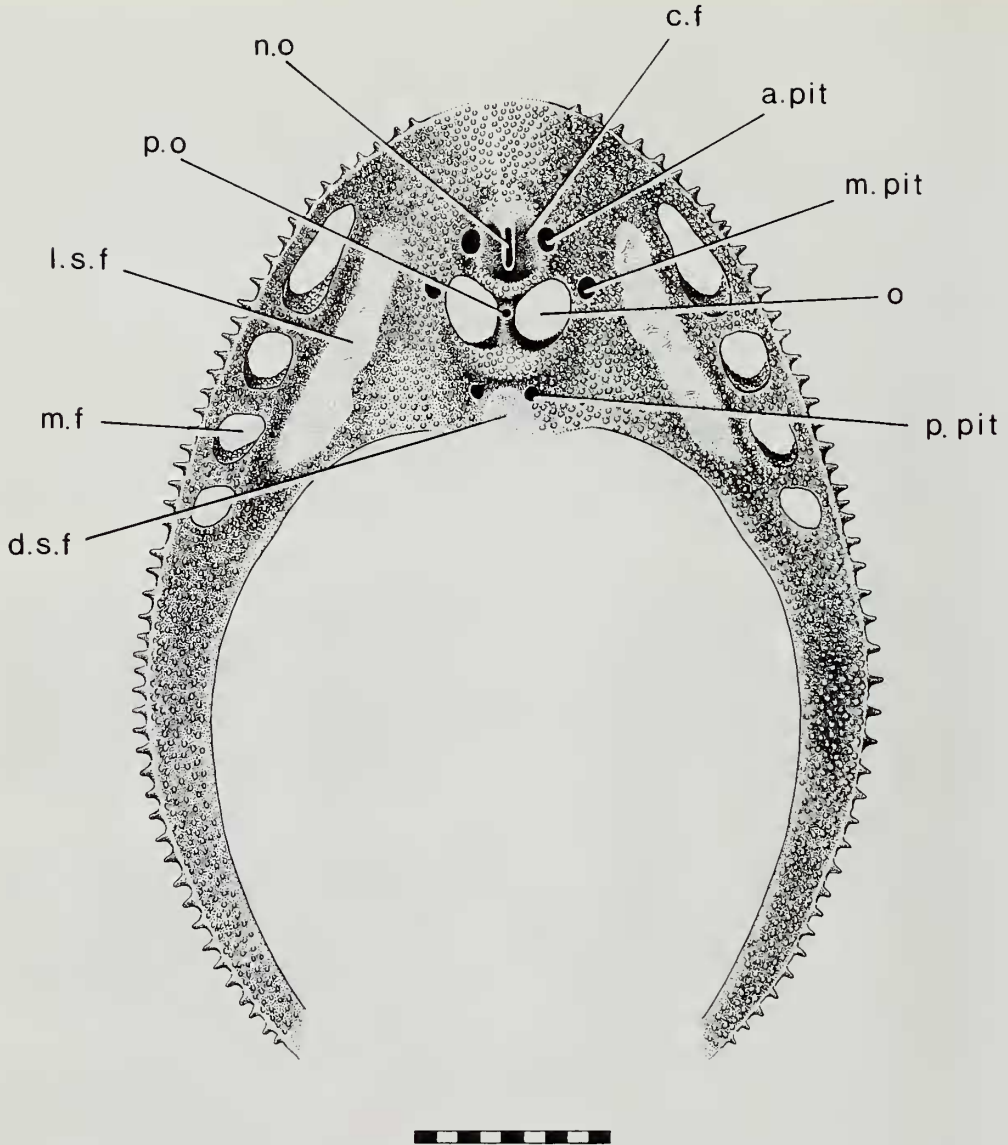
Fig. 2 *Sclerodus pustuliferus* Agassiz. Restoration of the cephalothoracic shield. Proportions based on BMNH P.9756. Scale bar in mm intervals.

equal size, in contrast to some other osteostracans where there is marked inequality between these openings (Janvier 1985*a*: fig. 59).

Several specimens show parts of the endocranial cavity, orbits and vestibular chambers, but all are poorly preserved so that only isolated details can be described. For the most part these details agree with those described for other osteostracans. The olfactory sac was housed within a deep recess (Fig. 5D) which forms the undersurface of the ridge between the orbits and the circumnasal fossa. More posteriorly, the grooves housing the anterior and posterior semi-circular canals, flanked by a groove for a large jugular vein, can be seen in BGS GSM 5150 (Fig. 4A).
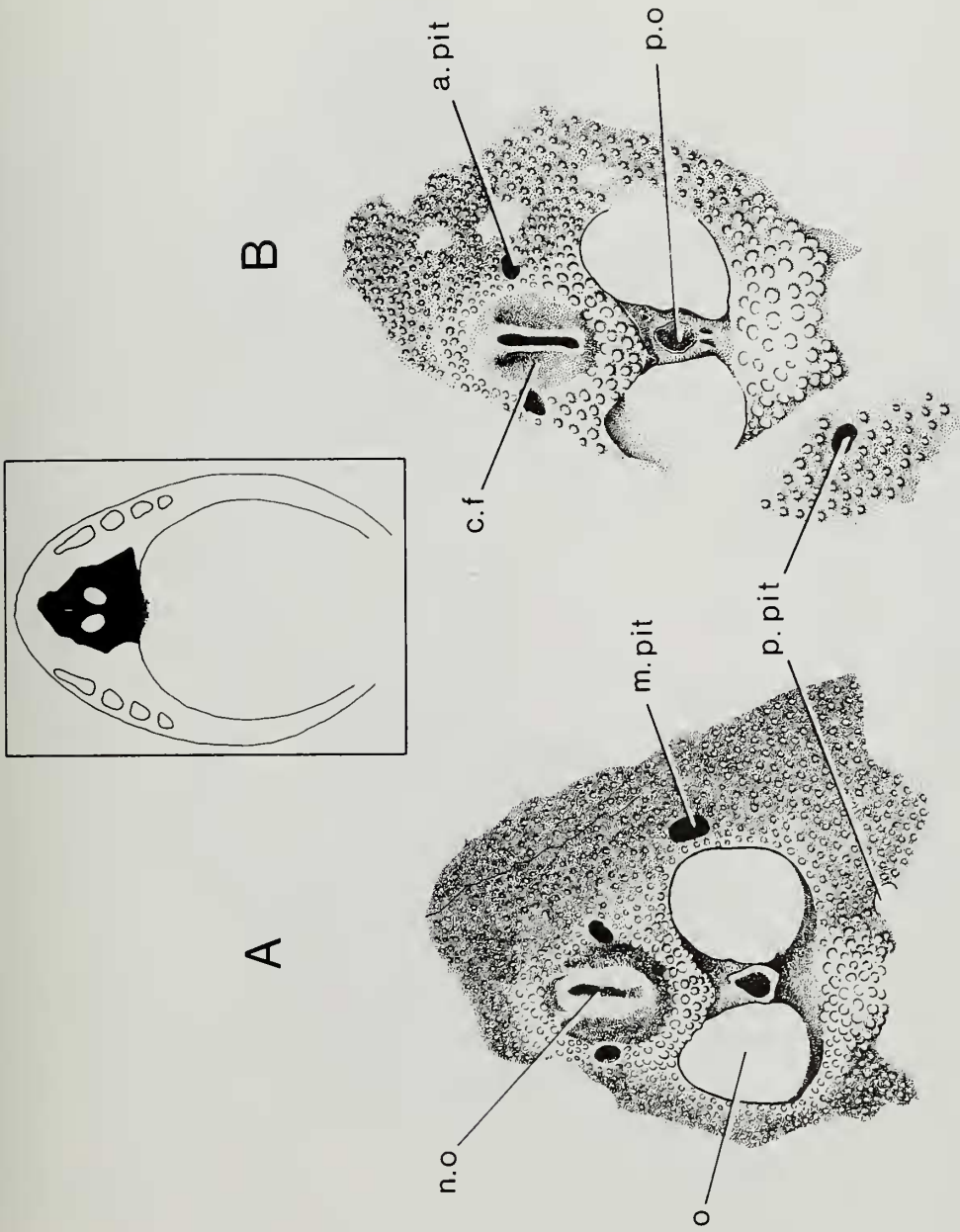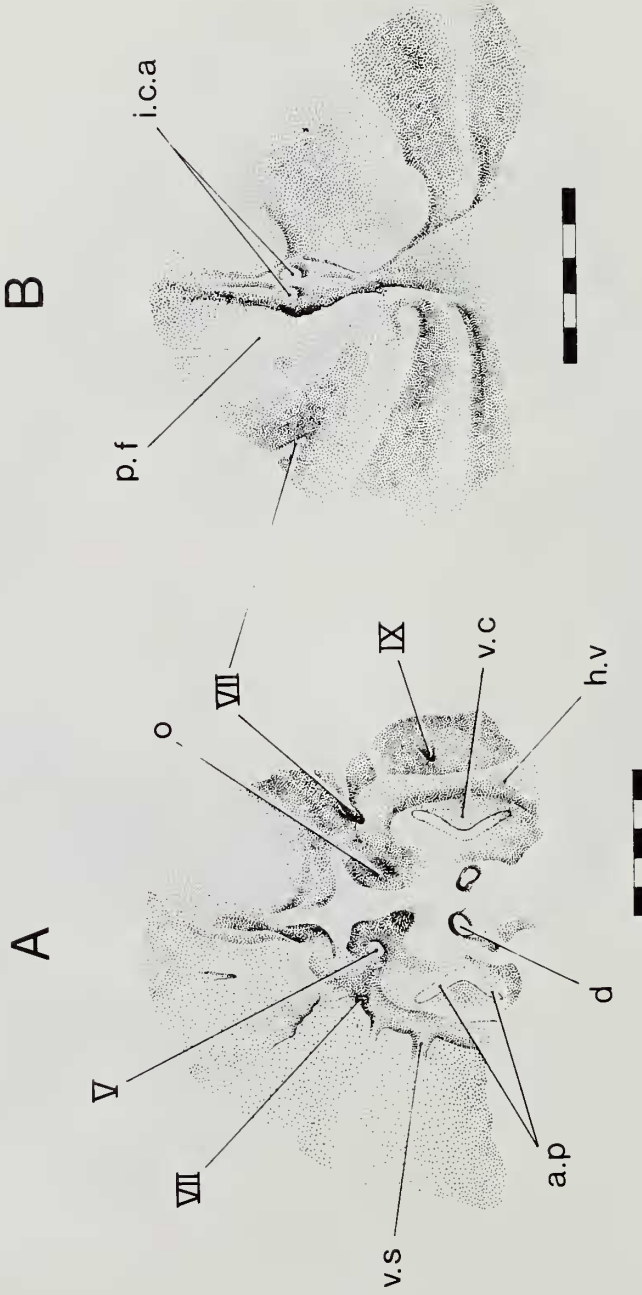
Fig. 3 *Sclerodus pustuliferus* Agassiz. Drawings of two specimens showing details of circumnasal fossa, pineal and orbital areas. A, BMNH P.27099. B, BMNH 35999. Scale bar in mm intervals.
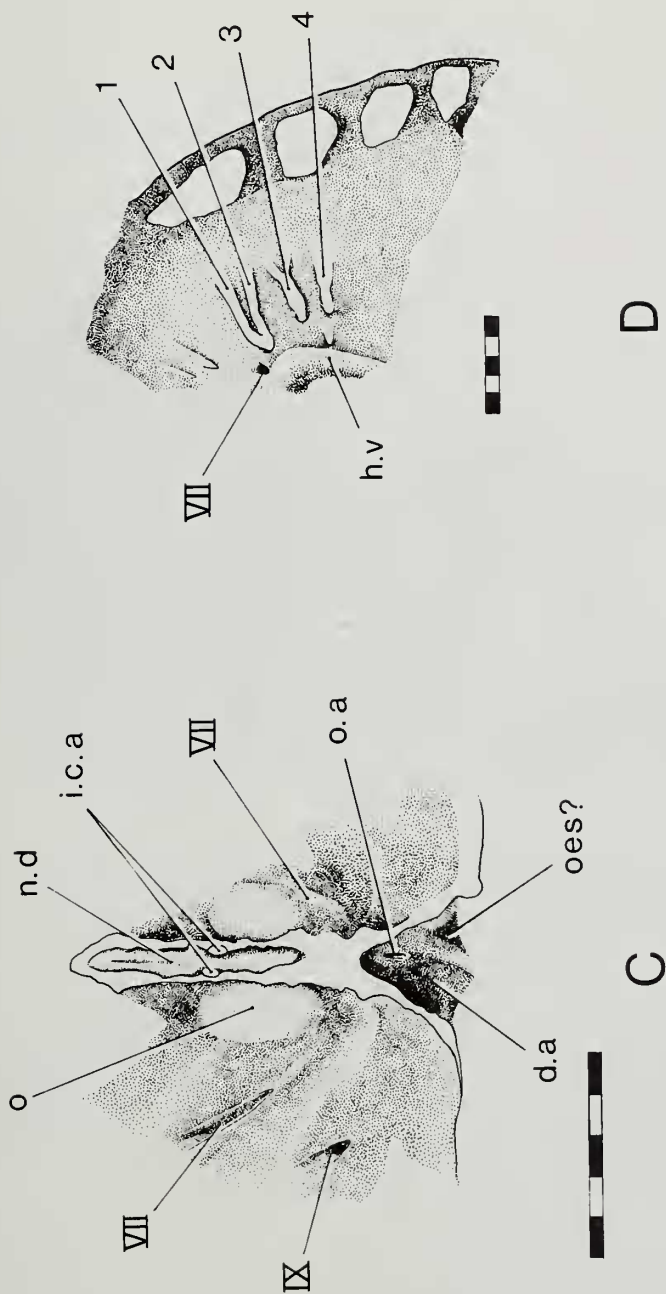
Fig. 4 *Sclerodus pustuliferus* Agassiz. Camera lucida drawings to show internal structures of cephalic shield as preserved in four specimens. A, BGS GSM 5150: dorsal view of brain cavity, floor of orbits and vestibular region. B, BGS GSM 21469: dorsal view of brain cavity and roof of oralobranchial chamber showing interbranchial ridges. C, BMNH P.9756: ventral view of central part of oralobranchial chamber showing orbital floor as swellings and ventral aspect of matrix-filled nasohypophysial duct; entire specimen illustrated by Stensiö (1932: pl. 53, fig. 5). D, BGS GSM 5149: dorsal view of right half of cephalic shield to show canals leading to lateral sensory field. Scale bars in mm intervals.

On the ventral surface the matrix infilling of the brain cavity suggests that the hypophysial duct is very long, reaching well back below the orbits and notched at the level of the anterior ends of the orbits by the entry of the internal carotid arteries (Figs 4B, C). The entry of the carotid arteries is asymmetrical, a fact which Janvier (1981b: 39) attributes to the constriction in this area caused by the proximity of the anterior cardinal veins. The material of *Sclerodus* is not good enough to comment on this suggestion. The floor of the orbit can be seen in BMNH P.9756 (Fig. 4C). Here it can be seen that the orbits of either side come into very close proximity with each other and may even meet, as in *Tremataspis* and *Oeselaspis* (Janvier 1985b: fig. 20). But there does not appear to be any medial recess of the posteroventral myodome (*sensu* Janvier 1981a; myodome of Stensiö 1927: fig. 28) such as is developed in most osteostracans (Janvier 1985a).

The posterior wall of the orbit is perforated by at least two foramina which lie close together and may be confluent (Fig. 5C). They are very unequal in size, the more dorsal being the smaller. They probably gave exit to the trochlearis above and the profundus below. The oculomotor may have entered the orbit through a small foramen lying near the floor and the medial wall. The floor and part of the rear wall of the orbit is perforated by a large foramen (Fig. 5C: V_2). I assume this is the trigeminal foramen through which V_2 and possibly VI passed. It probably also marks the place where the head vein entered the orbit, since there is no separate lateral foramen as in *Norselaspis* (Janvier 1981b: fig. 14A) or *Belonaspis* (Janvier 1977: fig. 7A). The path taken by the facial nerve marks the ventral surface of the orbit as a ridge (Fig. 4C) running anterolateraly immediately beneath the floor of the orbit.

Beneath the occipital region there is a triangular depression which pierces the postbranchial wall. It is best seen in BMNH P.9756 (Fig. 4C) and was labelled by Stensiö (1932: pl. 53, fig. 5) as the aortic groove. This is almost certainly correct, but the depression is of more complicated shape than implied by Stensiö. The depression (Fig. 4C) shows a deep groove which swings to the right as it passes posteriorly. This is typical for osteostracans and carried the dorsal aorta. The position of the issuing occipital artery may be indicated on the specimen illustrated (Fig. 4C, o.a). On the left side there is a shallower, shorter groove which appears to swing to the left. There are at least two interpretations of this groove: it could have housed the base of the subclavian artery (Janvier 1981b), or perhaps accommodated the oesophagus (Janvier 1984).

The orientation of the gill chambers is of the 'oligobranchiate' type as defined by Stensiö (1958). Only three branchial chambers are obvious on the specimens available (Fig. 4B) but there may well have been more, crowded posteriorly.

Sensory canal system. The sensory lines of *Sclerodus* are thought to have lain entirely superficial to the exoskeleton (Denison 1951b: 214) or to have been absent altogether (Stensiö 1932: 179). Certainly, no pit lines, grooves or pores mark the surface, a fact which Stensiö related to the absence of the superficial layer of the dermal skeleton. There are, however, other structures which may reasonably be interpreted as evidence of the sensory line system.

In specimens showing the orbital and nasohypophysial region there are often cup-shaped pits visible (Figs 3, 5, 6). Three pairs are consistently present (Fig. 3). The anterior is found at the level of the nasohypophysial opening and lies on or just outside the rim delimiting the circum-nasal fossa. The middle pit lies close to the orbital margin, roughly level with the middle of the orbit. The posterior pit lies just behind the postorbital swelling close to the edge of the dorsal sensory field. One or more of these pits may be seen in several specimens (BMNH 35999, 45949b, P.9756, P.27099, P.48704, P.58694, BGS GSM 5151 and BU 1992). These pits seem to have been overlooked by earlier investigators, since one or more are present in specimens used by Stensiö and Lankester. It is possible that those authors considered the pits to be preservational artifacts, as many specimens show breaks in the exoskeleton. Two more recently discovered specimens (BMNH P.48704 and especially P.58694), which show the pits particularly clearly, demonstrate that they are not artifacts. In both specimens the rim of the pits is perfectly regular and the smooth lining is pierced by one or more minute foramina (Fig. 5). The undersurface of the left anterior pit of BMNH P.58694 (Fig. 5D) shows that the foramina pierce the base of a longitudinal groove upon the visceral surface.
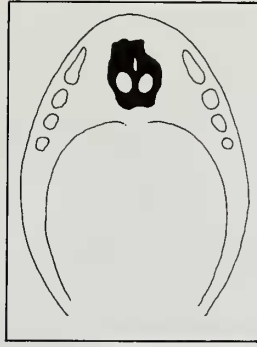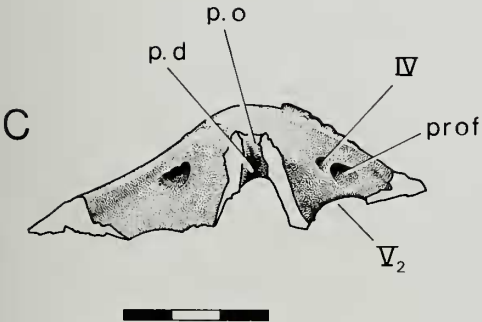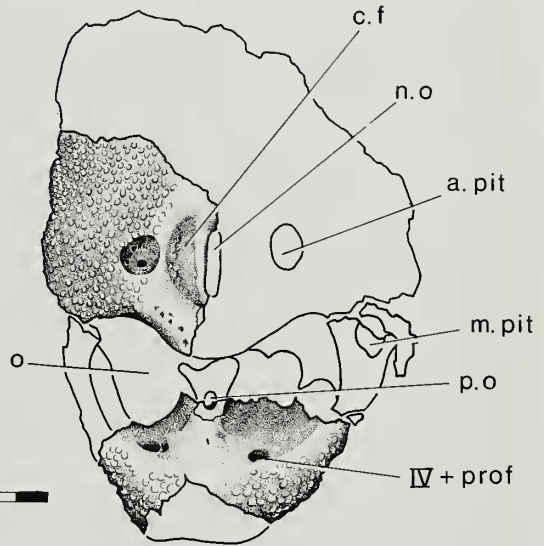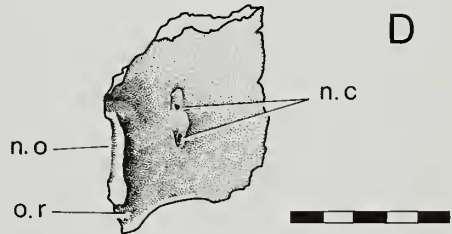
Fig. 5 *Sclerodus pustuliferus* Agassiz. BMNH P.58694, a specimen showing circumnasal fossa, orbits and pits: since its discovery the specimen has unfortunately been broken. A, specimen as originally collected—dorsal view, anterior towards top. B, drawing of remaining parts of specimen. C, anterior view of posterior wall of orbits. D, undersurface of fragment showing edge of naso-hypophysial opening and foramina piercing the floor of the anterior pit. Scale bars in mm intervals; note larger scale of C.

From the best preserved specimens it can be seen that each pit is ovoid to nearly circular in outline. The anterior and middle pits are of equal size and their longest diameter is about 75% as long as the nasohypophysial opening. The posterior pit is slightly smaller, being less than half the length of the nasophypophysial opening. In BMNH 45949b there is a further pit-like depression (Fig. 6A) located midway between the median line and the margin of the shield and at the transverse level of the posterior pit. This has been observed only on a single specimen, on one side only, and the borders of the pit are rather irregular; it thus may well be an artifact of preservation and it is not included in the restoration (Fig. 2).

Dr Janvier (personal communication) suggested that these pits may be the location of very large tubercles which have become lost during preservation. Longitudinal rows of enlarged dentine-capped tubercles are known in cladistically more derived thyestidians and, furthermore, Denison (1951b: fig. 35b) records that in *Thyestes verrucosus* Eichwald each tubercle is under-lain by a deep cavity. This idea is attractive and it would certainly be good evidence for associating *Sclerodus* with thyestidians. However, I consider that the pits are real surface structures for three reasons. No specimen of *Sclerodus* shows any sign of tubercles other than the small general surface tubercles; the rim of each pit is perfectly smooth and it tips into the cavity without break; and the floor is perfectly smooth and pierced by foramina.

Functional interpretation of these pits is hampered by the rarity of comparable structures in other fishes. No other osteostracan appears to have such pits, but comparison raises two possibilities. These pits may be an unusual development of the lateral sensory fields or they may be parts of the cephalic lateral line system. The first possibility seems unlikely because lateral fields, with their canal innervation, are present as in other osteostracans (see below). Also, the pits are wholly contained within the exoskeleton and therefore unlike sensory fields, vacuities passing completely through the exoskeleton and filled with small tesserae. The second possibility is more plausible. The floor of a pit (Fig. 5D) is pierced by a foramen of a size suggesting that nerves supplying neuromasts passed through. Furthermore, the pits are dis-posed in positions that, in thyestidians (*sensu* Janvier 1981b), would lie along the infraorbital line which lies close to the orbital margin and turns medially anterior to the nasohypophysial opening. I am therefore inclined to the view that these pits represent an unusual development of the sensory line system of *Sclerodus*.

Sensory fields and related s.e.l. (sinus expansion of the labyrinth) canals. There have been three different interpretations of the sensory fields of *Sclerodus* (Fig. 1). Lankester (1870: fig. 31) recognized only the dorsal field which he described as the postorbital valley. Stensiö (1932: fig. 62) identified both dorsal and lateral sensory fields, while Janvier (1975: fig. 5 *11*) restored a dorsal plus subdivided lateral fields.

This investigation agrees with Stensiö's results and suggests that *Sclerodus* possessed the usual osteostracan complement of single paired lateral fields plus a median dorsal field (Fig. 2). In no specimen are they clearly seen. The dorsal field is particularly poorly known. The anterior end is seen in BU 1992 where the margin is described by a low semicircular ridge and may (BMNH P.27099) be notched by the posterior sensory pit (Fig. 3A). The posterior limit of the dorsal sensory field remains unknown. Two specimens (BGS GSM 5150, and that figured by Stensiö, 1932: pl. 52, fig. 2) show paired canals leading from the vestibular region to the dorsal field area. Stensiö (1927: fig. 27A, *des*) has restored these canals for *Kiaeraspis* and Janvier (1977: fig. 9A, *c.c.s.d.*) for *Belonaspis puella*, and there is nothing to suggest conditions in *Sclerodus* were any different.

Evidence for the presence of lateral sensory fields is provided by breaks in the exoskeleton and traces of the canals (s.e.l. canals) which lead to them. The canals may be seen most clearly in BGS GSM 5149 (Fig. 4D) among available material and they were also recorded by Stensiö (1932: pl. 52, fig. 2). The partial counterpart of the specimen illustrated by Stensiö is BMNH 45949b and is also illustrated by the author (1932: pl. 52, fig. 1); it can be seen that by superimposing the two illustrations the s.e.l. canals run to just within the inner margin of the space labelled as the lateral sensory field.

The pattern of the canals is different in the two specimens. In the specimen illustrated by

Stensiö the first canal is double and branches close to the lateral field; this is very similar to the pattern in thyestidians, kiaeraspidians and benneviaspidians (*sensu* Janvier 1981*b*). But in BGS GSM 5149 (Fig. 4D) the branching of the first canal occurs midway between the level of the orbit and the lateral field area, a condition which Janvier (1985*a*) ranks as plesiomorphic for osteostracans. Since only two specimens of *Sclerodus* show evidence of the s.e.l. canals it is unwise to speculate on the significance of one or the other pattern, particularly since variation is known within other thyestidian taxa (Denison 1951*a*). It is, however, worth remarking that the facial nerve appears to run in front of the first canal. Stensiö illustrates five main canals and by comparing the relationship between the canals and the lateral fenestrations it appears that the posterior two are not seen in BGS GSM 5149, probably as a preservational defect. It also appears as though the s.e.l. canals radiate regularly from the otic region: that is, they are not branched into two distinct groups as they are in *Oeselapis* and *Tremataspis* where there are two separate sensory areas.

A number of other specimens (BMNH 45949b, P.9756, P.41095, BU 1992) show evidence of the lateral sensory field as depressions or irregularly-shaped vacuities in the exoskeleton (Fig. 7A). These specimens show that the sensory field stretched from the level of the first marginal fenestration to the third. The lateral border is quite distinct but the inner margin is somewhat irregular. The size and extent of the lateral field is similar to that seen in *Dartmuthia*, *Saaremaspis* and *Thyestes*.

The 'cornua'. Lankester (1870) and Stensiö (1932) both considered that the shield of *Sclerodus* continued posterolaterally on either side as long cornua. Stensiö believed that the 'cornu' bordered a pectoral fenestra containing a fin. A countertheory (Denison 1951*a*, Janvier 1975) suggests that the so-called 'cornu' is really only the lateral margin of the cephalothoracic shield, that there were no pectoral fenestrae containing fins and that the area between the 'cornua' was occupied by an unarmoured abdomen.

A number of observations suggest to me that the latter theory is correct. The 'cornu' is highly asymmetrical in cross section such that the ventral surface is flat, or nearly so, the dorsal and mesial surfaces are concave and the mesial edge is considerably deeper than the lateral edge. The cross-sectional shape looks like the sectioned edge of the cephalic shield. The lateral edge bears a single row of well-developed tubercles. The dorsal and ventral surfaces bear regular small tubercles. But tubercles are absent from the mesial surface which is instead perfectly smooth. These observations contrast with the cross-sectional aspect of true cornua as seen in most cornuate osteostracans. There, the shape is roughly symmetrical and is flattened, the surfaces are all convex to a greater or less degree, and the ornament continues on to the mesial surface and is usually developed as a series of enlarged tubercles.

The medial wall of the 'cornu' sweeps anteromedially to merge with the postbranchial wall. If a pectoral fin were present there should be some sign of insertion as seen in *Boreaspis* (Janvier 1977) or *Benneviaspis* (Janvier 1985*a*). But in two specimens (BMNH P.45315, BGS GSM 5149) showing this area clearly the bone is perfectly smooth.

One final observation is that the 'cornua' of *Sclerodus* are solid structures (Stensiö 1932: pl. 56, fig. 1). Large cornua, such as are seen in cephalaspids and scolenaspids, are penetrated by several large canals thought to have contained various blood vessels (Wängsjö 1952: fig. 17).

Thus, as restored, I believe that the area of the body between the 'cornua' was naked and suggest that the exoskeleton was coextensive with the endoskeleton. In both *Tremataspis* and *Oeselaspis* the endoskeleton of the cephalic portion curves posterolaterally to line the edge of the shield: the development of the endoskeleton is particularly extensive in *Didymaspis* (Janvier 1985*b*: fig. 19).

Lateral fenestrations. The lateral margin of the cephalic shield is marked with fenestrations. Lankester (1870: 58) considered that these fenestrations were cells within the exoskeleton and were therefore roofed and floored by bone. Stensiö (1927: 240) originally interpreted them as remnants of a much subdivided lateral sensory field, but subsequently changed his mind. Stensiö (1932) and Denison (1951*a*) considered they were true holes passing through the shield
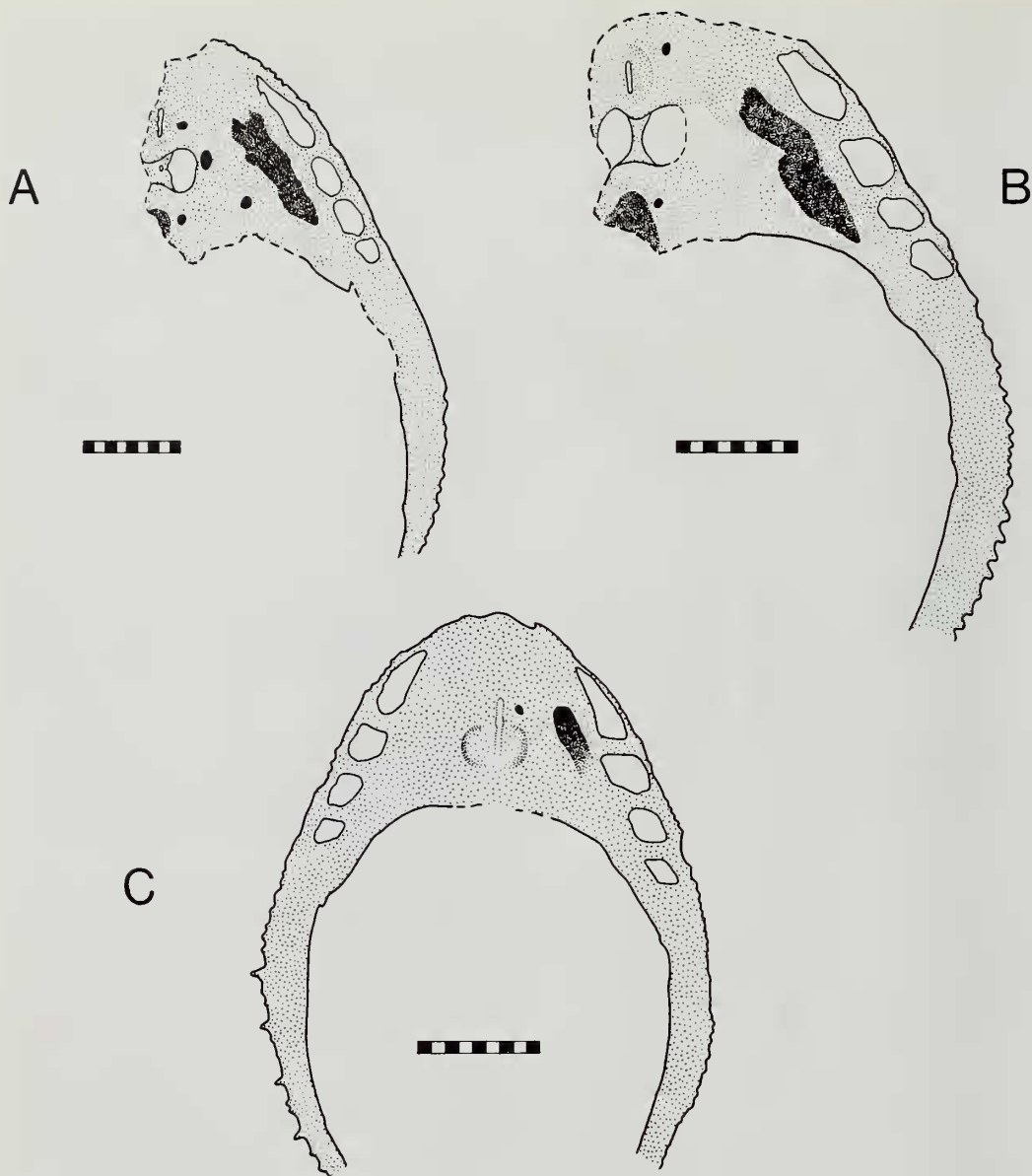
Fig. 6 *Sclerodus pustuliferus* Agassiz. Outline drawings of three specimens to show relative sizes and positions of nasohypophysial opening, dorsal and lateral sensory fields, pits and marginal fenestrations. A, BMNH 45949b, latex cast. B, BU 1992, latex cast. C, BMNH P.9756. Sensory fields–heavy stipple: area of shield–light stipple: sensory pits–black. Scale bars in mm intervals.

from top to bottom. Examination of specimens used in this study suggests this interpretation to be correct.

Fenestrae are seen clearly in many specimens, and where the lateral margin of the shield is complete it is obvious that there are four such fenestrae (BU 1992, BGS GSM 89283, GSM 21469, GSM 5149, GSM 5150, BMNH P.9752, P.9756, P.9757, P.9758, P.49015, 45949b).

Lankester (1870: fig. 31) showed six fenestrations, but none of the specimens used by him or any of the specimens used here show so many; the anterior two he showed are not present in any specimen. The most anterior fenestra is located at the transverse level of the naso-hypophysial opening and is elongate. The second, third and fourth become progressively smaller and more equidimensional (Figs. 2, 4D, 6, 7). The apparent regularity prompted an attempt to express the area of the posterior three fenestrae relative to the first (most anterior), which is always the largest in the series. The results obtained were very variable and this is probably because different specimens have been broken at different horizontal levels through the thickness of the shield. As an average of eight of the best preserved specimens, the area of the second fenestra is 75% of the first, the area of the third 56% and the fourth 46% of the first.

That the fenestrae passed right through the shield is not immediately obvious from the specimens available. The majority are preserved in dorsal view, in which it can be clearly seen that the ornament tips into the posterior walls of at least the anterior three fenestrae. Unfortunately the few specimens showing the ventral aspect are broken so it is not clear that the fenestrae reappear on the ventral surface. However, in these specimens the matrix infilling of the fenestrae stands well proud, implying considerable depth (P.49015, P.9756). The most direct evidence is provided by BMNH P.3247 (Fig. 7B). In this specimen the anterior end is broken through the last fenestra and it shows the walls of the fenestra passing without interruption from one surface to the other.

The posterior wall of each fenestration slopes anteroventrally and it appears that the slope is greatest within the anteriormost fenestra and becomes progressively more upright in more posterior fenestrae until the rear wall of the fourth fenestra is nearly vertical. Distortions of individual specimens preclude any attempt to measure precise angles. The anterior wall of each fenestra passes nearly vertically or only slightly anteroventrally through the shield. Several specimens (BMNH 45949b, P.9758, P.49015) show that the posterior wall of each fenestra, except perhaps the last, is ornamented with fine tubercles, considerably smaller than those covering the adjacent part of the shield. In BMNH 45949b (Fig. 7A) there is a clear line of division between the fine tuberculations lining the fenestra and the shield surface, suggesting that there may have been a small separate plate forming the rear wall of the fenestra, but this observation could not be confirmed on any other specimen. Despite this uncertainty the existence of an ornamented lining reinforces the view that they are true fenestrations rather than depressions or 'cells' within the structure of the bone.

The regularity of these fenestrae suggests that they were functionally important but it is difficult to be certain what this function may have been. There are no other osteostracans with such fenestrae, nor indeed are there many other animals showing such structures. The most obvious modern analogues are the marginal lunules in some clypeasteroid echinoids (sand dollars), the structure, evolution and possible functions of which have been discussed by Smith & Ghiold (1982). It is not possible to stretch comparison between lunulate echinoids and *Sclerodus* too far. There are quite considerable differences: unlike the fenestrations of *Sclerodus* the lunules of sand dollars are of roughly equal size, and in life they are partly filled with a thick epidermis containing spines and pedicellariae. Smith & Ghiold (1982) review the various hypotheses of echinoid lunule function. They are careful to point out that there may be a difference between the function of the anal lunule and the marginal lunules, which would be more comparable to those in *Sclerodus*. For the marginal lunules some seven hypotheses have been suggested (Smith & Ghiold 1982: 244–246). From their discussion those suggesting involvement with food gathering may be ignored. The most likely hypotheses for *Sclerodus* are hydrodynamic and, perhaps, assistance in burial, because these functions simply rely on lunule space and no associated epidermal structures. Furthermore the definite anteroposterior gradient in fenestra size (not seen incidentally in sand dollars) might suggest a hydrodynamic function.

Experiments on sand dollar tests have been carried out in wind tunnels and flume tanks (Telford 1981, 1983). It must be emphasized that these experiments treat the sand dollar simply as a geometrical shape, a fact which critics of hydrodynamic theories are quick to point out. But, accepting these parameters, the results indicate that the overall shape of a flat undersurface
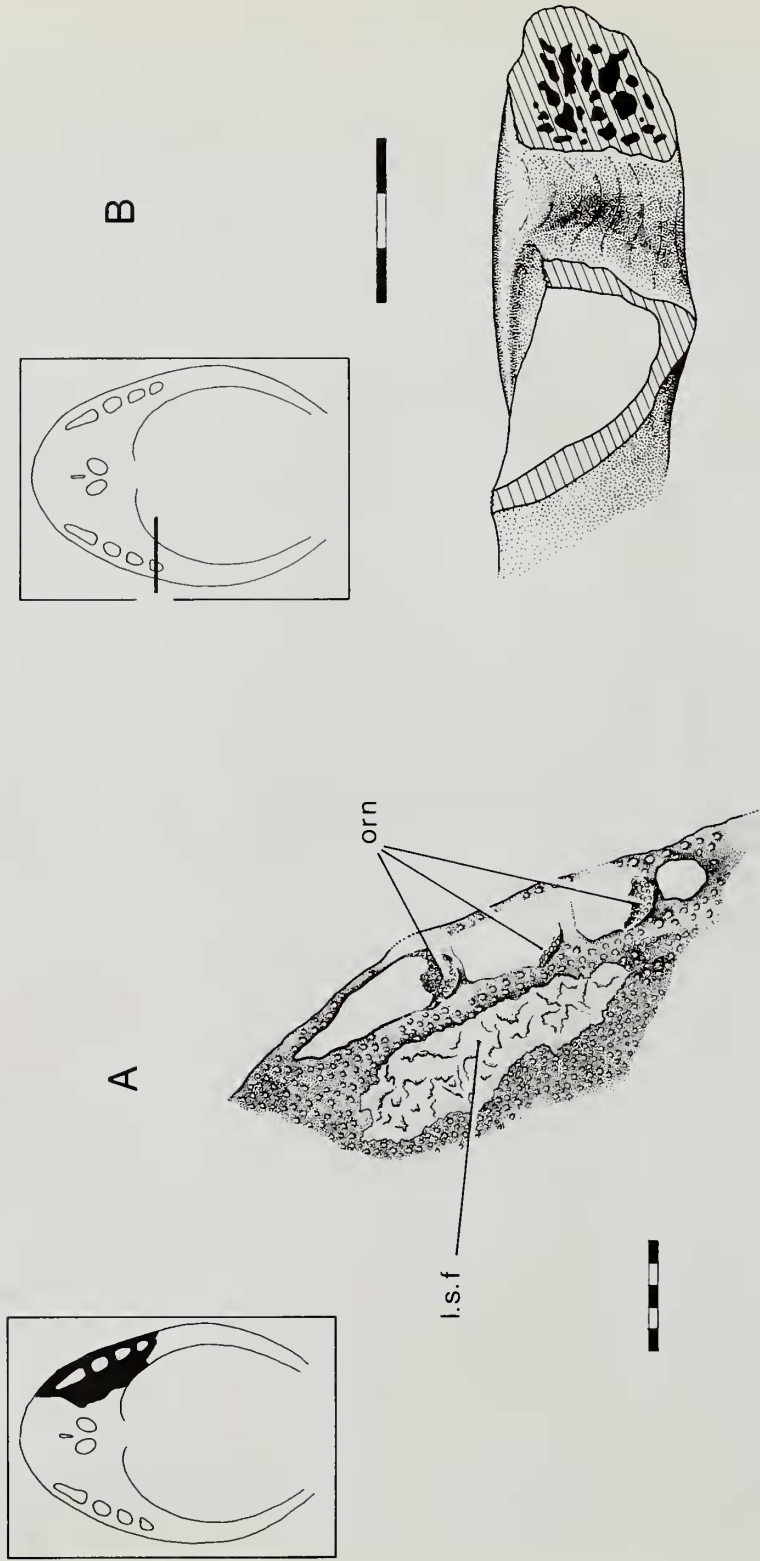
Fig. 7 *Sclerodus pustuliferus* Agassiz. A, drawing of latex cast of the edge of BMNH 45949b (Fig. 6A) to show lateral fenestrations with ornamented rear wall in at least the anterior three. B, BMNH P.3247, anterior view of broken 'cornu' showing rear wall of posteriormost fenestration. Scale bars in mm intervals.

and convex upper surface creates lift in a water current which is counteracted by the lunules. Some experiments (Telford 1983) suggest that the critical velocity (the water speed at which the sand dollar is lifted) might be increased by some 30%, implying that lunules could have a significant stabilizing effect; calculations made by Telford (1981: 619) suggest that moderate-sized sand dollars (7 cm diameter) may well experience critical velocities in many modern shallow water environments.

There is little point in trying to perform similar experiments on a *Sclerodus* model since the shield is only part of the animal. But it is possible that the fenestrae provided some similar stabilizing function appropriate to a fish presumed to have lived in littoral waters and presumably subject to varying water speeds. The sectioned shape of *Sclerodus* is certainly that which would create lift if left uncompensated.

Relationships of *Sclerodus*

In this paper *Sclerodus* is placed in the family Tremataspididae. This requires some explanation in view of the very different hypotheses of relationships of *Tremataspis* and allies (Westoll 1945; Denison 1951a; Halstead 1982, 1985; Halstead Tarlo 1967; Janvier 1981a, 1985a, b, c) and the fact that *Sclerodus* is often placed in its own monotypic family.

The assignment of *Sclerodus* to a distinct family (Sclerodidae Berg 1940, Sclerodontidae Fowler 1947) is no more than a recognition of its uniqueness, which cannot be denied, but does not imply much about relationship. Stensiö (1932: 176) suggested it to be closely related to *Thyestes* and *Didymaspis* because the facial nerve (called V_2 by Stensiö) runs anterior to the first s.e.l. canal. This character is now known to be more widely distributed (*Procephalaspis*, *Witaaspis*, *Oeselaspis*, *Tremataspis*) but may still be significant, depending on whether one rates these taxa as constituting a monophyletic (Janvier 1981b), polyphyletic (Denison 1951a) or paraphyletic group (Halstead Tarlo 1967).

Denison (1951a: fig. 31) regarded tremataspids (*Didymaspis*, *Tremataspis*, *Saaremaspis*, *Dartmuthia*) as an ancestral group from which at least four different lineages of osteostracans evolved. Denison (1951a: 180) acknowledged that his group Tremataspidae was not necessarily a natural assemblage but that it only emphasised '. . . the convergence towards a central ancestral type'. He arrived at his conception of the ancestral type by determining polarity of several different character transformations using stratigraphical occurrence as the arbiter. Thus, he observed that the majority of Ludlovian osteostracans have small lateral fields, relatively few s.e.l. canals and a short prepineal region; the converse conditions would be derived. He admitted that the stratigraphical occurrence did not resolve whether the primitive osteostracan shield was long or short, or whether paired fins were primitively present or absent. But he decided that because *Tremataspis* showed the primitive condition of lateral fields, s.e.l. canals and prepineal length, then a long shield and absence of paired fins must also be primitive.

Denison's is the most clearly reasoned advocacy of the stratigraphical argument and the primitiveness of tremataspids, a view shared by Westoll (1945, 1985) and Halstead Tarlo (1967). *Sclerodus* shares many of these 'primitive' features such as a long carapace, short prepineal region, no paired fins or cornua and relatively short lateral sensory fields. But *Sclerodus* cannot be classified with tremataspids purely on the basis of 'primitive' features, since on these terms it would only mean that *Sclerodus* looked something like the ancestral osteostracan.

Janvier (1985a, b, c) has criticized this stratigraphical approach to character phylogeny in osteostracans by pointing out that forms such as *Ateleaspis*, with paired fins and large lateral fields, and *Procephalaspis*, with cornua and paired fins, occur contemporaneously with or even earlier than *Tremataspis*.

Halstead (1985) introduced another line of argument by claiming that *Tremataspis* shows a primitive geometry of the cephalic shield since, in gross outline, it resembles a cyathaspid heterostracan. If this doubtful reasoning is to mean anything then, presumably, its import lies in character distribution. Thus, if it could be shown that the *Tremataspis/Cyathaspis*-shaped shield was widely distributed amongst primitive members of the jawless fish groups then there might be some justification in assuming it to be a generalized feature. However, irrespective of

which proposed phylogeny of jawless fishes one accepts (Forey 1984: fig. 3) the 'primitive' nature of the *Tremataspis/Cyathaspis* geometry cannot be justified on grounds of commonality.

If stratigraphy and commonality fail us then we are left with congruence of character distribution as the overriding criterion of choice: this has been the line of argument adopted by Janvier (1981*a*, *b*; 1985*a*, *c*). He concludes, like Stensiö, that *Tremataspis* and traditionally-accepted related genera are derived osteostracans. Janvier's approach is cladistic classification and he has attempted to determine plesiomorphic and apomorphic states, and then to check these against congruence. Janvier (1985*a*) suggests that non-cornuate genera such as *Ateleaspis* and *Aceraspis* are primitive because they exhibit micromery on the undersurface of the head, broad-based pectoral fins not flanked by cornua, and two dorsal fins. These features are generalized, based on outgroup comparison. Using this assumption Janvier's phylogeny of osteostracans (1985*a*: fig. 69) rates tremataspids as derived cornuate forms which have second-arily lost pectoral fins, reduced the number of s.e.l. canals and developed an elongate carapace. Furthermore, Janvier considers that the sister-group of tremataspids is *Thyestes*, with forms such as *Witaaspis*, *Auchenaspis salteri* and *Procephalaspis* as progressively more plesiomorphic forms. He refers to this entire assemblage as thyestidians.

Janvier's thyestidians include tremataspids as well as forms which Denison (1951*a*: fig. 31) regards as ancestral to the Ateleaspidae (non-cornuate osteostracans with paired fins) and Cephalaspidae (including benneviaspidians). Janvier's classification with respect to tremataspids agrees with Stensiö (1958), and is almost the antithesis of that of Denison (and also Halstead Tarlo 1967). In reaction to some recent criticism (Westoll 1985, Halstead 1985) Janvier (1985*c*: fig. 36) translated Denison's (1951*a*) tree into a cladogram and detailed some 14 incongruous character distributions which result.

I was interested to see what might happen if some of the data presented by Janvier (1985*a*, *c*) were subjected to cladistic computer analysis using PAUP (Phylogenetic Analysis using Parsimony) version 2.2, a program prepared by Dr David Swofford, which is designed to select the most parsimonious tree or trees which can be rooted to follow the fate of different character transformations. I chose to look at 16 taxa with respect to 27 characters. Some of them were higher taxa (cephalaspidians, kiaeraspidians, scolenaspidians, benneviaspidians, tremataspids *sensu stricto*), and it was therefore assumed that these groups are monophyletic. This may, of course, be disputed but Janvier (1985*a*) has discussed the arguments and I find his reasoning sound. More importantly, the advocates of competing theories also accept these groups (Denison 1951*a*, Halstead Tarlo 1967). Groups about which there is argument include the Ateleaspidae (*Ateleaspis*, *Aceraspis*, *Hirella*, *Hemiteleaspis* and *Hemicyclaspis*) and osteostracans traditionally associated with *Tremataspis* (*Auchenaspis*[1], *Witaaspis*, *Thyestes*, *Didymaspis*). Denison (1951*a*) and Ritchie (1967: 79) regarded the Ateleaspidae as monophyletic and derived from *Witaaspis* or the tremataspid *Saaremaspis*. Janvier, however, regards ateleaspid genera as primitive osteostracans forming a paraphyletic assemblage, with some being more nearly related to cornuate osteostracans than to other ateleaspids. In other words, for this analysis I have chosen to designate separate genera in those areas where classifications are substantially different.

Another problem area is character designation. As Janvier (1985*a*) implies in his classification there are several well-defined groups of osteostracans, but there is a problem of identifying characters to link groups other than those which are general to osteostracans. Thus, there may be polychotomies within osteostracan classification simply because there are no identifiable characters to resolve the issue further. This is a problem distinct from conflicting character distribution. The final difficulty stems from the uncertainty of distinguishing polarity of charac-ter state transformations. This is, of course, the source of most disagreements between conflict-ing classifications (see above) and is particularly difficult to resolve in an extinct group such as osteostracans.

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[1] For many years *Auchenaspis* and *Thyestes* have been regarded as synonyms (Woodward 1891: 195). Janvier (1985*a*: 122), however, retains *Auchenaspis salteri* Egerton and *Auchenaspis egertoni* Lankester as distinct from *Thyestes verrucosus* Eichwald. Janvier recognizes several synapomorphies of *Thyestes verrucosus* and Tremataspididae not present in species of *Auchenaspis*.

The most obvious features which can be compared amongst osteostracans are size, shape and complexity of the dorsal and lateral sensory fields, the canals leading to them and their relationship to cranial nerves. Additionally, there is variation in the development of the cornua and the trunk shield. Understandably, classifications have used these features. But since non-osteostracans do not have sensory fields or related canals, and the cornua are not easily compared with the skeletal outgrowths in other groups (e.g. spinals of placoderms or the cornual plates of pteraspidiform heterostracans), the polarity of many features associated with these structures is not resolvable by outgroup comparison.

The computer program built the 'tree', paying no regard to the entered polarity even though the data had been scored, in large part, in agreement with Janvier's assessment of primitive (0) or derived (1). The derived characters used in the program were:

1. Pectoral fins present, as evinced by sinus and/or area of attachment. Presence of pectoral fins in *Didymaspis* after Janvier (1985*a*).
2. Dorsal field separated from pineal plate. Converse condition—pineal plate contacting dorsal field—regarded as plesiomorphic within osteostracans. There are some intragroup exceptions where, for instance, nearly all members show one condition (e.g. benneviaspi-dians show pineal contacting the dorsal field) with one species (*Benneviaspis holtedahli* Stensiö) showing the derived condition.
3. Tesserae on undersurface of oralobranchial chamber. The plesiomorphic condition is micromery where there is a shagreen of minute scales exemplified in, for instance, *Atel-easpis*. Like Janvier (1984, 1985*a*) I feel confident about the polarity of this character since micromery (covering of small, equal-sized and regular-shaped units) is widespread amongst agnathan groups and primitive gnathostomes. The tesserate condition is, on the other hand, regarded as derived and is exemplified by *Saaremaspis* (Janvier 1985*b*: fig. 16) or *Hemicyclaspis murchisoni* (Egerton) (Stensiö 1932: pl. 7, fig. 3). Here the covering of the oralobranchial chamber is made up of *irregularly*-sized and *irregularly*-shaped units.
4. Pineal plate equidimensional or longer than broad. There are some intragroup exceptions which must be regarded as secondary reversals. For example, tremataspids generally show the derived condition but *Timanaspis* is exceptional.
5. Pineal plate absent. There are some intragroup exceptions; for instance, amongst cephal-aspidians, which generally have a well-developed plate, this has been secondarily lost in *Hildenaspis* and *Mimetaspis*.
6. Orthobranchiate condition.
7. Pattern of branching of the first canal leading to the lateral sensory field. There are three conditions (Janvier 1985*a*: 107) but the polarity of transformation is by no means clear. For this reason the character is scored quite arbitrarily here: 0 = branching near lateral field, 1 = branching midway between eye and lateral field, 2 = branching near orbit.
8. Abdomen with scale-covered ventrolateral crest.
9. Cornual process. The development of the cornual process is regarded as a derived condi-tion. There are problems with identifying a cornual process in kiaeraspidians but I follow Janvier (1981*b*) in believing the cornual process to be primitive for that group.
10. Long abdominal division of cephalothoracic shield (more than two segments incorporated into the shield).
11. Facial nerve running alongside or in front of first canal to the lateral sensory field.
12. Abdominal part of shield closed ventrally (may be secondarily reduced in extent in some, e.g. *Nectaspis*).
13. Branchial nerves penetrating gill chamber laterally. The condition of this character is only known sporadically throughout osteostracans.
14. Extrabranchial divisions large.
15. Opening of endolymphatic duct lying outside dorsal sensory field. The converse condition is considered plesiomorphic because it is more widely distributed amongst osteostracans. Some benneviaspidians and also *Didymaspis* have openings on the edge of the sensory field; these are considered to show the plesiomorphic condition.

16. Lateral sensory fields not extending greatly beyond level of nasohypophysial opening.
17. Lateral sensory fields reaching posteriorly well beyond level of dorsal sensory field.
18. Lateral sensory fields posteriorly expanded.
19. Supraoral fields with denticles. Condition is only known sporadically throughout osteostracans.
20. Anterior dorsal fin or fin scale absent. This character is regarded as unquestionably derived. Most primitive members of agnathan groups have two dorsal fins.
21. Solid rim to the shield.
22. Infraorbital line stopping short of lateral sensory field.
23. Posteroventral 'myodome' absent. See Janvier (1985a: 77) for discussion.
24. Infraorbital line running close to circumnasal fossa.
25. Paired fins constricted at base or separated from trunk scales.
26. Horizontal perforated lamina within the sensory canals of the middle layer of exoskeleton.
27. Enameloid layer.

The data matrix, as given in Table 1, includes the characters used by advocates of opposing hypotheses. The difference is that Janvier would choose *Ateleaspis* as the root of the tree whereas Denison, Westoll and Halstead would favour tremataspids. So the computer program was run twice using a different root. On each occasion there were 60 equally parsimonious trees, this being a reflection of the relatively poor quality of the data (approximately 30% homoplasy, and some possible dichotomies unsupported by characters—see below). The consensus trees (the common element of the 60 most parsimonious trees) are shown in Fig. 8 where the root is fixed at *Ateleaspis* on the left and tremataspids on the right.

The first observation is that the computer-generated tree, based on parsimony and using tremataspids as ancestor, is not at all like the tree advocated by Halstead Tarlo (1967) as illustrated in Fig. 9. Halstead Tarlo's tree is less highly resolved and, potentially, there may be considerably more dissimilarity between the two solutions presented in this figure: the major areas of difference may, however, be briefly mentioned. Halstead Tarlo's tree ranks cephalaspidians, kiaeraspidians and benneviaspidians as a trichotomy and as the most derived osteostracans. The consensus tree ranks these as successively more plesiomorphic sister-groups

Table 1 Character data matrix for 16 osteostracan taxa. For explanation of characters see text. A, *Ateleaspis*; B, *Aceraspis*; C, *Hirella*; D, *Hemiteleaspis*; E, cephalaspidians; F, kiaeraspidians; G, scolenaspidians; H, benneviaspidians; I, tremataspids; J, *Procephalaspis*; K, *Auchenaspis salteri*; L, *A. egertoni*; M, *Witaaspis*; N, *Thyestes*; O, *Didymaspis*; P, *Hemicyclaspis*.

| Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
A	1	0	0	0	0	0	?	1	0	0	?	0	0	0	0	?	0	0	0	0	0	0	?	0	0	0	0
B	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0	0
C	1	0	1	0	0	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	1	0	0
D	1	0	1	0	?	0	?	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	?	0	1	0	0
E	1	0	1	0	0	0	2	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
F	1	1	1	0	?	1	0	1	1	1	0	1	1	1	0	0	0	0	0	?	1	1	1	0	1	0	0
G	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0
H	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0	0	1	0	?	1	1	0	0	1	0	0
I	0	1	1	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1
J	1	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0	?	1	1	1	1	1	?	0
K	1	0	1	0	0	0	0	1	1	0	1	1	0	?	0	1	0	0	0	?	1	1	1	?	1	1	?
L	1	0	1	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	0	1	1	1	1	?	1	1	?
M	1	1	1	1	0	0	0	1	0	1	1	1	0	?	1	1	0	0	0	?	1	1	1	?	1	1	1
N	1	1	1	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1
O	1	1	1	0	1	?	0	?	?	1	1	1	0	?	0	1	0	0	0	?	1	1	1	?	0	?	?
P	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	1	0	0
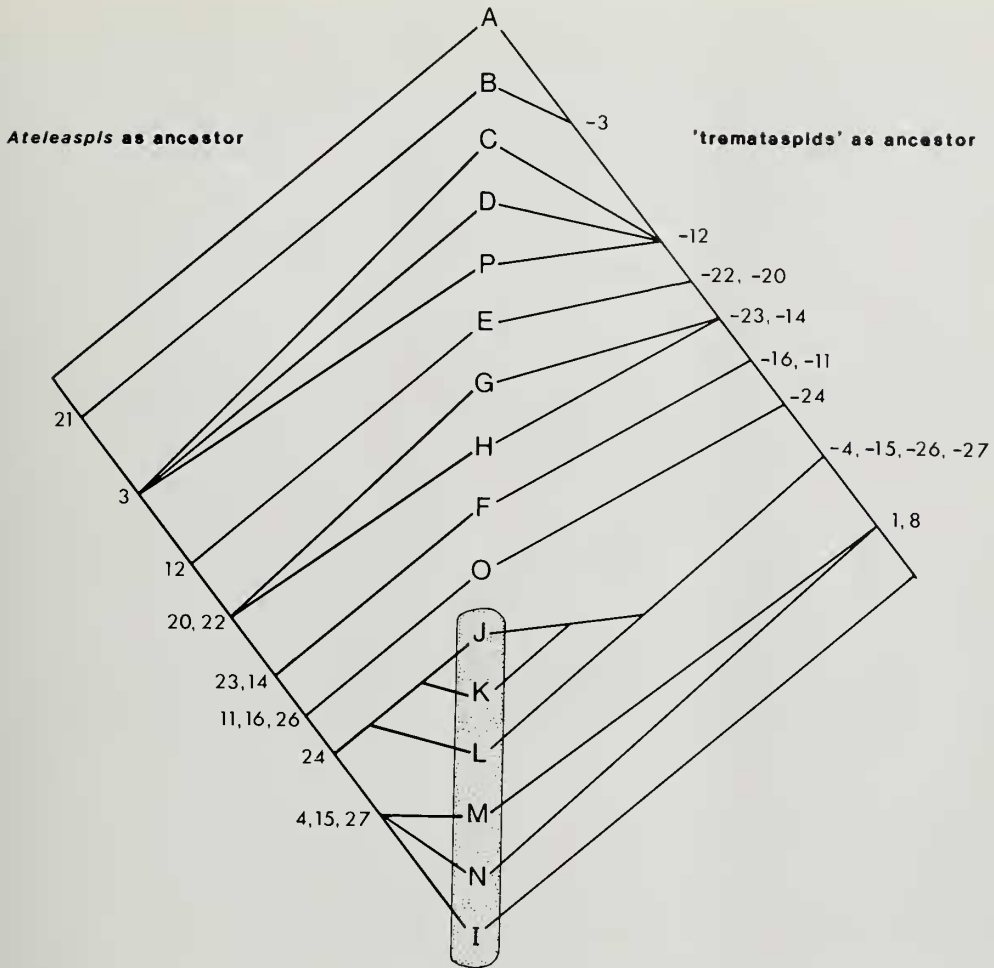
Fig. 8 Consensus tree produced from the 60 most parsimonious alternative solutions. Topography of the trees is identical. Left–the root placed at *Ateleaspis*. Right–the root placed at tremataspids. Only those characters treated as synapomorphies are shown. Taxa A–P as in Table 1. Numbers refer to characters detailed in text. Particular taxa under consideration are enclosed within stippled area.

to the Ateleaspidae. *Thyestes* occupies a very different position, being a derived taxon and the sister-group to cephalaspidians + kiaeraspidians + benneviaspidians in the Halstead Tarlo tree, while in the consensus tree it is the sister-group to all other osteostracans with the exception of tremataspids. Thus, whatever else the Halstead Tarlo tree might contain, it does not approach a parsimonious solution given the data used here (Fig. 9).

In Fig. 8 only the characters used once (synapomorphies) are applied to the diagrams. Those against the 'tremataspids as ancestor' tree are largely indicated as negative features, but this is a consequence of the way in which the characters were coded in the first place. Perusing this list we may note that some characters (11, 15, 16, 24, 26) are only found in osteostracans and it is therefore difficult to establish polarity. But one prediction of fixing the root at tremataspids is the deduction that the primitive osteostracan developed a complex horizontal lamina within the exoskeleton which was subsequently lost by most osteostracans. The alternative assumption
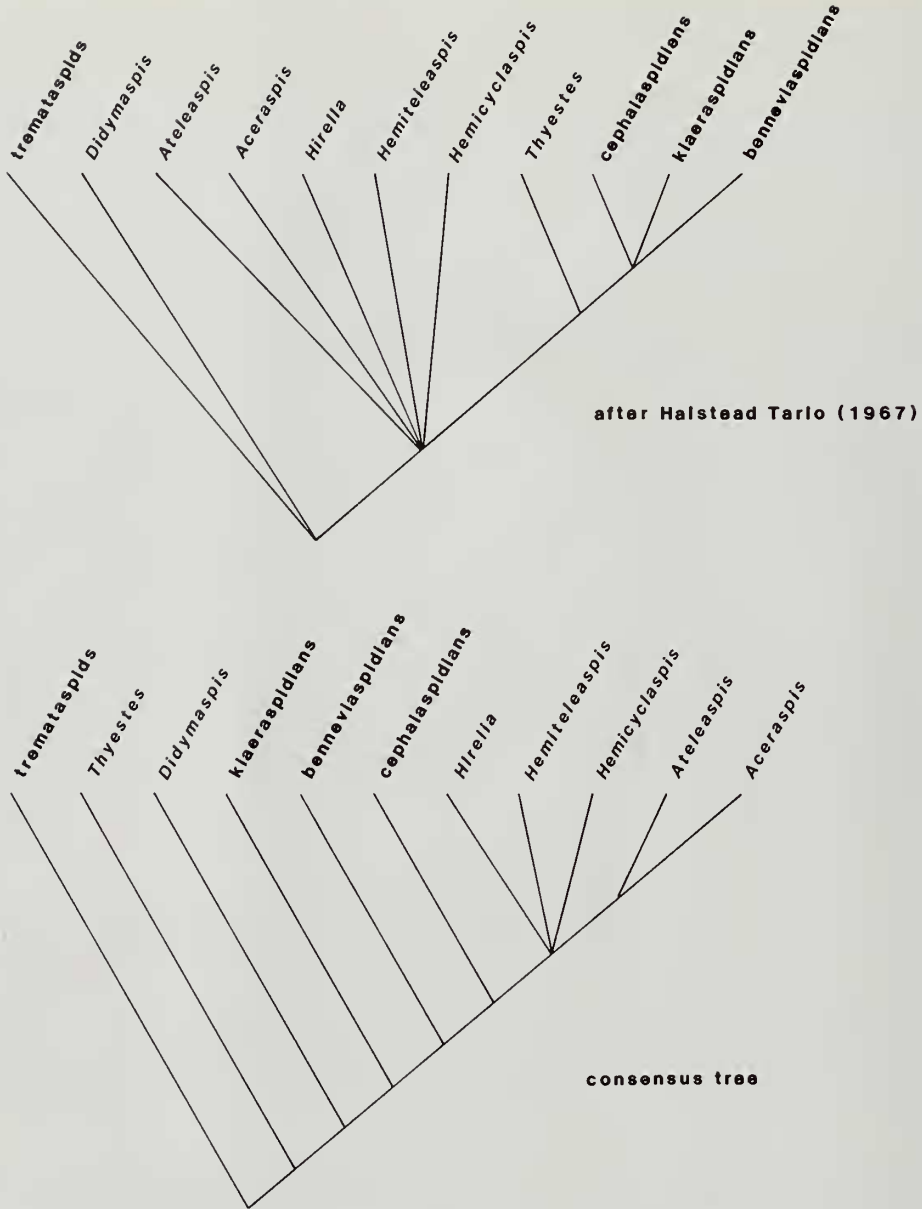
Fig. 9 Tree of osteostracan taxa produced by Halstead Tarlo (1967) compared with computer consensus tree rooted at tremataspids.

(*Ateleaspis* as ancestor) rates this character as an acquisition within a small group of osteostracans and so appears a more plausible alternative.

My main reasons for preferring the '*Ateleaspis* tree' centre on the behaviour of characters 3, 12 and 20. I believe that micromery is a primitive condition and that the tesserate (3) condition is derived. The micromeric undersurface of *Ateleaspis* and *Aceraspis* may be associated with the very small trunk scales in these forms which is probably also a plesiomorphic feature (Janvier 1985a: 106). I also believe that the ventral enclosure of the abdominal region (12) is a derived

condition. And, finally, I consider that the presence of two dorsal fins (20) is a plesiomorphic feature, this being found in lampreys, some placoderms and the more primitive acanthodians. Many osteostracans have enlarged dorsal scales in place of one or both dorsal fins. Janvier (1984) uses the presence of such scales as a character. For instance, in the solution given in Fig. 10, Janvier would suggest that a character linking *Hemicyclaspis* and cladistically more derived taxa would be the presence of a modified scale in place of the anterior dorsal fin. This is perfectly acceptable and would be one way of resolving what is otherwise a trichotomy between some ateleaspidian genera (Fig. 8). It should also be noted that the presence of paired fins is here regarded as plesiomorphic for osteostracans, based on a higher level phylogeny which ranks gnathostomes and osteostracans as sister-groups (Janvier 1981*c*, Forey 1984).

In Fig. 10 one of the 'Ateleaspis trees' is given in full and all characters (except no. 7— branching of s.e.l. canals) are included. It can be seen that the node linking *Hemicyclaspis* and cladistically more derived osteostracans is not supported by any characters, and that linking *Hemiteleaspis* and more derived osteostracans is only supported by character 7 which is very difficult to evaluate. These areas of uncertainty give rise to many of the alternative trees and are probably better depicted as a polychotomy incorporating *Hemiteleaspis*, *Hemicyclaspis*, *Hirella* and cladistically more derived taxa. The inclusion of additional characters (e.g. inferred modification of the anterior dorsal fin) may partially resolve this polychotomy.

Another area in which alternative trees varied concerns benneviaspidians, scolenaspidians and cladistically more derived osteostracans. The solution shown in Fig. 10 suggests benneviaspidians and scolenaspidians to be sister-groups, based on the common possession of posteriorly-expanded lateral sensory fields (18). The alternative solution ranks benneviaspidians as the sister-group to cladistically more derived forms, with scolenaspidians as the plesiomorphic sister-group. This is the solution preferred by Janvier (1985*a*), who bases it on the fact that in benneviaspidians and cladistically more derived forms the first s.e.l. canal branches near the lateral sensory field. The trichotomy shown in the consensus tree (Fig. 8) is therefore the result of conflicting character distributions which may only be resolved by discovering more characters.

Character 7—the branching pattern of the first s.e.l. canal—was entered as a multistate character, but the resulting transformations implied by the computer tree were very ambiguous. The primitive condition was fixed with reference to the condition in *Aceraspis* (see also Janvier 1985*a*), in which the canal branches midway between the eye and the lateral sensory field. A transformation of this presumed general condition in *Hemiteleaspis* and cladistically more derived forms shows branching very near the orbit (best exemplified in cephalaspidians). An even more restricted grouping—scolenaspidians, benneviaspidians and their sister-group— show transformation to a canal which branches near to the lateral field. Scolenaspidians show a reversal to 'primitive' conditions.

None of the conditions of the branching pattern is coextensive with any of the groups specified in Fig. 10. This character might therefore need re-examination in the light of the classification proposed here. In view of the fact that it is sometimes difficult to be certain whether the canal branches midway between the eye and the lateral field or whether it is nearer one than the other, and of the fact that there may be variation within a single species (p. 13), this character is not considered further even though it has traditionally been used in classifications of osteostracans.

Characters 5, 6, 13, 17 are treated as parallelisms. The behaviour of character 6 (orthobranchiate condition) is perhaps interesting. This is a character, used by Stensiö (1958), which might suggest that kiaeraspidians and benneviaspidians are sister-groups (see alternative in Janvier 1981*b*: fig. 43), but none of the computer-generated trees suggested this grouping.

The last area of uncertainty within the computer-generated tree concerns tremataspids, *Witaaspis* and *Thyestes*. The solution shown here (Fig. 10) ranks tremataspids and *Witaaspis* as sister-groups based on the secondary loss of the cornual processes (9). The alternative solution places tremataspids and *Thyestes* as sister-groups because of the common possession of a denticulated supraoral field (11). Neither character is clear cut: it is sometimes very difficult to be certain whether cornual processes are short or absent altogether, and the condition of the
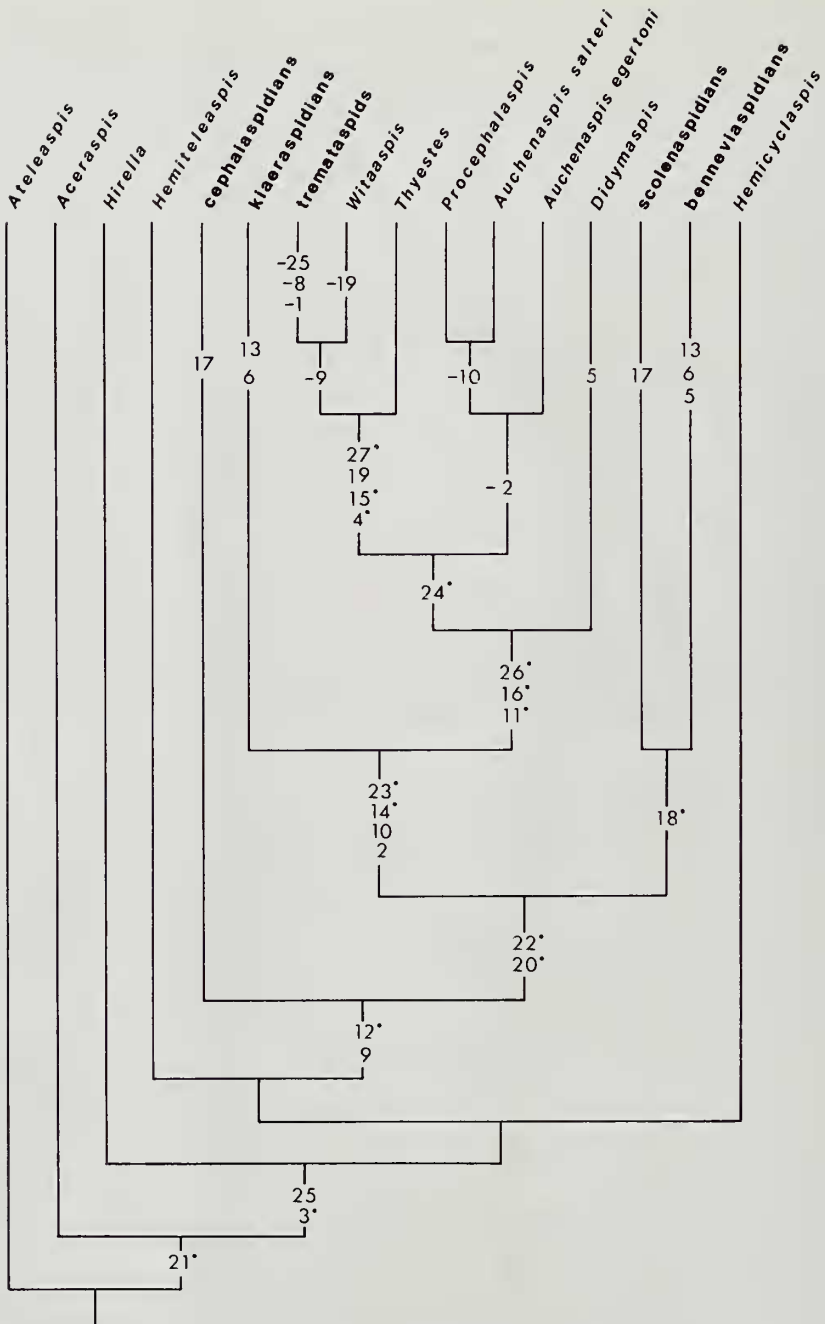
Fig. 10 One of the 60 most parsimonious trees rooted at *Ateleaspis* with all characters and charac-
ter transformations shown. Synapomorphies designated with 'prime dot'. Other characters are
parallelisms or reversals (minus signs). Character 7 omitted. See text for list and discussion of
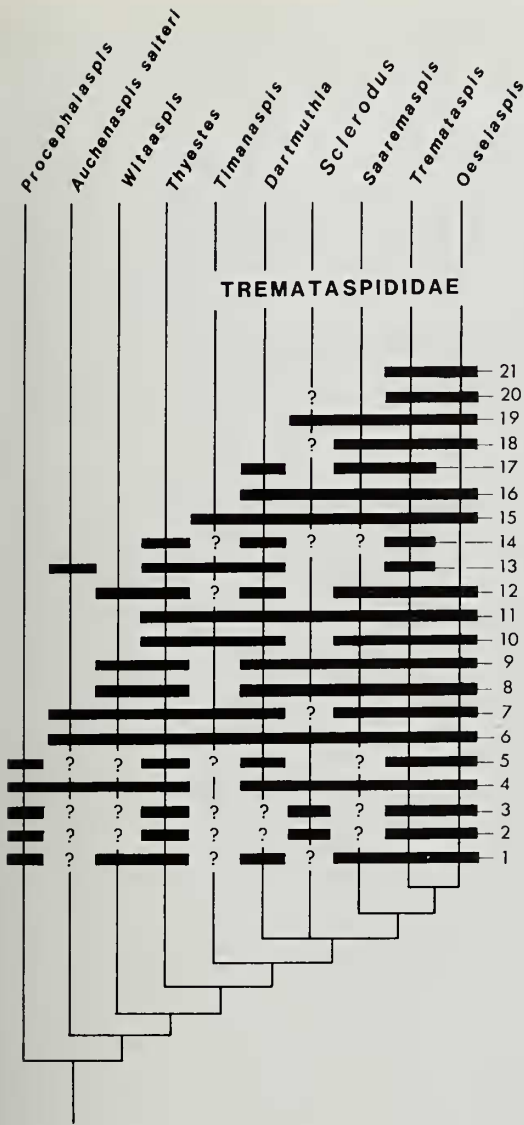characters.

Fig. 11 Systematic position of *Sclerodus* inserted in a phylogeny of thyestidians produced by Janvier (1985*c*: fig. 40) with synapomorphies specified by that author—his numbering is used here. The synapomorphies are as follows: 1–infraorbital sensory canal running close to orbit and circumnasal fossa, 2–canal for facial nerve not running in orbit, 3–medial recess of posteroventral myodome absent, 4–pineal plate narrow or short, 5–horizontal lamina developed within exoskeleton, 6–abdominal division long or very long, 7–openings of endolymphatic ducts outside dorsal sensory field, 8–pineal plate very short, 9–dorsal sensory field separated from pineal recess, 10–nasohypophysial opening short or very short, 11–abdominal division very long, 12–superficial enameloid layer developed, 13–longitudinal rows of enlarged tubercles developed, 14–supraoral field triangular with denticles, 15–absence of paired fins, 16–circumnasal fossa deep and elliptical, 17–'cosmine' forming a continuous layer, 18–dorsal sensory field very short, 19–circumnasal fossa very short, 20–dorsal sensory field extremely short, 21–lateral sensory field divided into two parts. See text for discussion.

supraoral field is poorly known in many osteostracans. Janvier (1985*c*: fig. 40) prefers the second solution; he suggests that, in addition to the denticulated supraoral field, *Thyestes* and tremataspids show a slightly longer abdominal division and a shorter nasohypophysial opening. I find these characters difficult to evaluate, but they could be one way of resolving a trichotomy shown in the consensus tree. The important conclusion to be drawn is that, despite the differences between the computer-generated tree and Janvier's classification (1985*a*: fig. 69), both firmly support thyestidians as a group.

The implication for discussion about the interrelationships of *Sclerodus* is that I feel entitled to regard Tremataspididae as a monophyletic taxon to which additional taxa can be added in pectinate fashion as specified by Janvier (1985*a, c*); see Fig. 11. There are, as Janvier freely admits, some problems with this classification; the greatest is perhaps incomplete knowledge of

morphology in certain forms. But given these constraints, *Sclerodus*, which is particularly poorly known, can be placed within the Tremataspididae as the sister-group of *Dartmuthia*, or of *Saaremaspis*, *Tremataspis* and *Oeselaspis*. These conflicting solutions are shown as a trichotomy in Fig. 11.

With respect to the cladogram of thyestidians produced by Janvier (Fig. 11), *Sclerodus* agrees in showing the synapomorphies numbered 2, 3, 9, 15, 16. Characters numbered 4 and 8 refer to the shape of the pineal plate, or the pineal recess when the plate has never been found (as in *Sclerodus*). These two characters are really differing degrees of development of the same feature and *Sclerodus* would appear to match that specified under character 8 most closely, exemplified by *Witaaspis* and *Thyestes*. Character 1—medial course of the infraorbital line—depends on interpretation of the pits within the shield (see p. 12). Characters numbered 6 and 11 refer to progressive lengthening of the abdominal shield which is also seen in kiaeraspidians. *Sclerodus* certainly shows a long abdominal division but this is only developed laterally.

Characters 7, 18, 20 refer to the size and shape of the dorsal sensory field, while character 14 concerns the supraoral field. These structures are unknown or too poorly known in *Sclerodus* to assess their status. Character 13 (longitudinal rows of enlarged tubercles), absent in *Sclerodus* (see p. 13), must be considered as a reversal. Character 21 (divided lateral sensory fields) is known to be absent; but the status of this character as a synapomorphy must be questioned since it is present in kiaeraspidians.

Characters 5, 12, 17 refer to details of histology, an aspect in which *Sclerodus* appears unique in several respects. There is one further feature of *Sclerodus* which recalls conditions in thyestidians. The lateral head vein (Fig. 4A) runs well outside the vestibular chamber and makes a broad medial sweep at the level of the orbit. This feature has not been considered in the above discussion on osteostracan classification because this part of the anatomy remains poorly known in most species.

Conclusions

The comparative information available for *Sclerodus* suggests that it is a member of the Tremataspididae, which is here accepted as a monophyletic group.

The Appendix (opposite) lists the stratigraphical occurrence of the *Sclerodus* specimens used in this study. In addition to this *Sclerodus* has been reported from the Ludlow Bone Bed of Brook House, Llangibby, Gwent; Downton Castle Sandstone of Beech Hill Farm, Usk, Monmouth; also Turners Hill (Temeside Beds), south Staffordshire (Ball 1951). Thus, *Sclerodus* is restricted to the Downtonian of the Anglo-Welsh depositional basin. It is also apparent that, even allowing for collecting bias at long-known and well-collected sites such as the Ludlow Bone Bed exposure at Ludford Lane, Ludlow, Shropshire, the majority of the specimens are found in the Ludlow Bone Bed and in the lower part of the Downton Castle Sandstone. Very few have been found in the overlying Lower Red Downton Group or its equivalent, the Temeside Shale. Even the listing of the specimens from Wallop Hall as coming from the Temeside Shale may have to be revised, to place them in the Downton Castle Sandstone (Dr J. B. Richardson, personal communication). This, and the evidence of the associated fauna and sedimentological features, indicate that *Sclerodus* was a marine fish becoming rare with the onset of brackish water conditions (Allen & Tarlo 1963).

The vertebrates most commonly associated with *Sclerodus* are acanthodians, *Cyathaspis banski* and thelodonts. In terms of Turner's (1973) thelodont faunas *Sclerodus* would be part of the upper part of the *Thelodus parvidens* fauna. Osteostracan congeners are *Auchenaspis* (*Thyestes*) and *Hemicyclaspis*, which are found in all but the lowermost levels of the Downton Castle Sandstone, and *Didymaspis* which appears in the overlying Lower Red Downton Group. Thus, *Sclerodus* is the earliest osteostracan to appear in the Anglo-Wesh basin and is one of the truly marine osteostracans. It appears to be the ecological equivalent of the Wenlock and Ludlovian thyestidians from Estonia which Märss & Einasto (1978) suggest occupied shallow lagoonal waters shoreward of sand-belt facies. Janvier (1985c: 211) suggested that *Tremataspis* and other derived tremataspids inhabiting these Baltic waters may have been burrowing forms.

These osteostracans have rather convex ventral surfaces such that the cross-sectional profile would be elliptical. I do not think that *Sclerodus* showed such a convexity; rather it is possible that it was able to submerge itself beneath the loose surface sand, and that the marginal fenestrae may have helped in this activity.

Acknowledgements

Appendix

Material examined in the course of this study is listed below. The specimens are of very different quality and a mere listing of numbers might be misleading, so they are divided into three categories denoting different parts. Within each category the specimens are arranged stratigraphically, beginning with Ludlow Bone Bed, then overlying Downton Castle Sandstone, then Temeside Shale/Lower Red Downton or presumed equivalent.

Cephalic shields including details of orbit, nasohypophysial opening, brain etc.:
Ludlow Bone Bed, Ludford Lane, Ludlow, Shropshire—BMNH P.48704, BGS GSM 89284 (Lankester 1870: pl. 13, figs 10, 10a) and counterpart GSM 5151.
Ludlow Bone Bed, Forge Bridge, Downton Castle estate, Shropshire—BMNH P.58694.
Downton Castle Sandstone, Ludford Lane, Ludlow, Shropshire—BMNH 45949b (Lankester 1870: pl. 13, fig. 14; Stensiö 1932: pl. 52, fig. 1), 45949e, P.9756 (Stensiö 1932: pl. 53, fig. 5), BGS GSM 5150 (Lankester 1870: pl. 13, fig. 12), GSM 89283.
Downton Castle Sandstone, Kington, Hereford & Worcester—BMNH P.9752, P.31857, BGS GSM 89285, BU 1992.
Downton Castle Sandstone, Onibury (Norton), Shropshire—BMNH 35999, P.27099, BGS GSM 5149, 21469, 21470.
Temeside Shales, Wallop Hall, Shropshire—BMNH P.49015.

Portions of cephalic shields only showing marginal fenestrae:
Downton Castle Sandstone, Ludford Lane, Ludlow, Shropshire—BMNH 45949f, 45962, P.9757, P.9758.
Downton Castle Sandstone, Kington, Hereford & Worcester—BMNH P.5044, P.25403, BGS GSM 57541, GSM 89298.
Downton Castle Sandstone, Onibury (Norton), Shropshire—BGS GSM 89296.
Downton Castle Sandstone, Shobdon, Hereford & Worcester—BMNH P.25401.
Downton Castle Sandstone, Presteigne, Powys—BMNH P.31745.

'Cornua':
Ludlow Bone Bed, Ludford Lane, Ludlow, Shropshire—BMNH 45970b, c, P.3247 (Stensiö 1932: pl. 53, fig. 1), P.7360, P.25204, P.32255.
Ludlow Bone Bed, Clun, Shropshire—BMNH P.39559, P.39562, P.39572-6, P.49016.
Ludlow Bone Bed, Rushall, Woolhope, Hereford & Worcester—BMNH P.53119.
Downton Castle Bone Bed, Lucton, Hereford & Worcester—BMNH P.8927.
Downton Castle Sandstone, Ludford Lane, Ludlow, Shropshire—BMNH 45949 (Lankester 1870: pl. 13, fig. 11), 45949c, d, 45973 (Stensiö 1932: pl. 56, fig. 1), P.9897 (Stensiö 1932: pl. 53, fig. 3), P.25203 (Stensiö 1932: pl. 53, fig. 2).
Downton Castle Sandstone, Kington, Hereford & Worcester—BMNH P.25402, BGS GSM 5152.
Downton Castle Sandstone, Downton Bridge, Shropshire—BMNH 45970, 45970a.
Downton Castle Sandstone, Onibury (Norton), Shropshire—BMNH P.9897 (Stensiö 1932: pl. 53, fig. 3).
Temeside Shales, Wallop Hall, Shropshire—BMNH P.48954.
Temeside Shales, Baggeridge Colliery, south Staffordshire—P.17383-4.

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